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DR LEO CLARKE (Orcid ID : 0000-0002-1600-6197)

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LOW-COST TOOLS MITIGATE CLIMATE CHANGE DURING REPRODUCTION IN AN ENDANGERED MARINE ECTOTHERM

Clarke, L.J.[1], Elliot, R.L. [1], Abella-Perez, E.[2,3], Jenkins, S.R.[1], Marco, A.[2], Martins, S.[3] & Hawkes, L.A.[4]

[1] School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey, LL59 5AB, UK

[2] Estacion Biologica de Donana (CSIC), C/ America Vespuccio, s/n, 41092 Sevilla, Spain

[3] BIOS.CV, Sal Rei, Boavista, Republic of Cape Verde

[4] University of Exeter, College of Life and Environmental Sciences, Hatherley Laboratories, Streatham Campus, Exeter, Devon EX4 4PS, UK

* Corresponding author: l.clarke@bangor.ac.uk

Tel: 01248 388141

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Abstract

1. The impacts of anthropogenic climate change will be most dramatic for species that live in narrow thermal niches, such as reptiles. Given the imminent threat to biodiversity, and that actions to reduce carbon emissions are not yet sufficient, it is important that a sound evidence base of potential mitigation options is available for conservation managers.
2. Successful incubation and production of male sea turtle hatchlings is threatened by increased global temperatures (sex is determined by the temperature at which eggs incubate). Here we test two conservation tools to reduce incubation temperatures: clutch splitting and clutch shading, on a nesting loggerhead turtle (*Caretta caretta*) population in the Eastern Atlantic Ocean.
3. During the thermosensitive period of incubation, split and shaded clutches were both 1.00 ˚C cooler than control nests. Clutch splitting (mean: 45 eggs) reduced nest temperatures by reducing metabolic heating during incubation compared to controls (mean: 92 eggs). Modelled primary sex ratios differed between nest treatments, with 1.50 % (± 6 % S.E.) females produced in shaded nests, 45.00 % (± 7 % S.E.) females in split nests and 69.00 % (± 6% S.E.) females in controls. Neither treatment affected hatchling size, success, mass or vigour. When clutch splitting was repeated two years later, hatch success was higher in split clutches compared to controls.
4. *Synthesis and Applications*: Clutch splitting and clutch shading successfully altered the thermal profile of incubating turtle nests. When there is sufficient knowledge to better understand the effects of intervention on fundamental population demographics, they will be useful for reducing incubation temperatures in sea turtle nests, potentially increasing nest survival and male hatchling production. The effect of clutch splitting in reducing nest temperature was lower relative to clutch shading, but requires significantly less funding, materials and specialist skill, key factors for management of turtle rookeries that are often in remote, resource-limited areas.

Introduction

1.1 Climate change and effects on biodiversity

Conserving global biodiversity in a rapidly changing climate is one of the most significant challenges currently faced by conservationists and practitioners. The International Panel on Climate Change (IPCC, 2018) predicts increases in global mean surface temperatures of 3.7 to 4.8 °C by 2100 unless significant mitigation effort is expended, and biodiversity is on the brink of a sixth mass extinction event (Barnosky *et al.*, 2011; Panetta et al., 2018). The effects of this rapid and unprecedented shift in the Earth's climate will be particularly dramatic for species that live and function within narrow temperature ranges and climatic niches (Sodhi *et al.*, 2008; Rijnsdorp *et al.*, 2009; Bellard *et al.*, 2012), and there has been a recent increase

in efforts to adapt existing conservation management to incorporate climate change effects (Heller & Zavaleta, 2009; Hagerman *et al.*, 2010; Shoo *et al*., 2013). Such efforts include the mitigation and reduction of non-climatic threats, increasing species connectivity, maintaining and increasing genetic diversity, protection of climate resilient refugia and translocation of species (Chambers *et al.*, 2005; Heller & Zavaleta, 2009). To date, these efforts have largely focused on terrestrial species (Feeley *et al*., 2017), although impacts on marine biodiversity are increasingly documented (Poloczanska *et al*., 2016, Worm & Lotze *et al.,* 2016; Tittensor *et al*., 2019).

1.2 Marine Turtles and Climate Change

Global climate change will particularly affect reptiles, as multiple life history stages are strongly influenced by environmental factors (Sinervo *et al.*, 2010; Ihlow *et al.*, 2012; Bohm *et al*., 2016). In particular, reptiles' reproductive biology is intrinsically linked to the thermal environment, with nesting phenology, inter-nesting intervals, incubation duration, hatching success and hatchling sex and fitness all influenced by environmental temperature (Braña & Ji, 2000; Clusella-Trullas *et al.*, 2011; Buckley *et al.*, 2012; Sim *et al.*, 2015).

Marine turtles are already of conservation concern and in addition to non-climatic stressors such as fishing bycatch, plastic pollution and poaching (Wallace et al., 2011), increased global temperatures will likely carry significant population implications (Hamann *et al.*, 2007; Poloczanska *et al.*, 2009; Hawkes *et al*., 2009; Abella-Pérez *et al*., 2016; Fuentes & Saba, 2016). Forecasted warming will lead to extremely female-biased offspring and reduced hatching success, which may compromise both viability and survivorship of some populations (Fuentes *et al.*, 2009; Mitchell & Janzen, 2010; Witt *et al.*, 2010; Laloë *et al*., 2014; Hays *et al*., 2017). Indeed, highly-feminised sex ratios (Hays *et al.*, 2014; Laloe *et al*., 2014; Hays *et al.*, 2017; Tanner *et al*., 2019) and reduced hatching success (Tomillo *et al*., 2012; Montero *et al*., 2018) have been documented in various populations in recent years.

With work demonstrating limited adaptive potential (Monsinjon *et al.*, 2019; Tilley *et al.*, 2019), it is prudent to investigate potential mitigation strategies for biodiversity management (Hawkes *et al.*, 2009). Past studies on marine turtles have investigated the use of artificial shading of nests, laboratory egg incubation, watering of incubating clutches and even the addition of paler and thus less infra-red absorptive sediments to beaches as management interventions (Hamann *et al.*, 2010; Fuentes *et al.*, 2012; Patino-Martinez *et al.*, 2012; Wood *et al.*, 2014; Jourdan & Fuentes, 2015; Liles *et al*., 2019). Many of these strategies require substantial financial and/or labour investment and may be resource intensive. As the majority of marine turtle nesting takes place in resource-scarce, developing countries, ideal strategies ideally should be simple and cheap (Esteban *et al.*, 2018).

1.3 Aims

To inform potential strategies for the mitigation of climate change effects to marine turtles, we investigated two potential nest intervention approaches to reduce nest incubation temperatures: (1) clutch splitting; and (2) clutch shading. We also tested whether these approaches; (3) could significantly alter the primary sex ratio produced and (4) whether they could be achieved without compromising hatching success and hatchling size or vigour. Finally, we discuss the potential ramifications of intervening in such life history metrics.

Materials and Methods

2.1 Study Area

The study took place on the island of Boa Vista, Cabo Verde, West Africa, the world's second largest nesting aggregation of loggerhead sea turtles (*Caretta caretta*; (Marco *et al*., 2012; Laloë *et al.*, 2019)). Around 65% of nests in this population are laid on the island of Boa Vista (Laloë *et al.*, 2019) (Figure 1).

2.2 Nest Collection

Nesting females were encountered between 7th and 13th July 2012 and 24th July and 10th August 2014 and clutches (n=136) were relocated to a 12 x 50 m beach front hatchery within six hours of laying. In 2012, eggs were relocated to a hatchery at Ervatao beach, run by the Natura 2000 turtle conservation project, and in 2014, to a hatchery at the nearby Joao Barrosa beach run by the BIOS.CV NGO conservation project. Each hatchery was natural sand and ran alongshore, reaching the spring high tide line at its lowest point, representing a realistic natural nesting environment. Clutches were reburied at 45cm depth (the bottom of the nest); the average for loggerhead nests on Boa Vista Island (Abella-Pérez *et al.*, 2007; Marco *et al.*, 2018).

2.3 Mitigation Strategies

In 2012, 60 clutches were collected and allocated equally to three treatments. First, 20 clutches (range: 66 to 111 eggs (mean 88.35 ± 0.75 S.E.; Table 1)) were reburied in the hatchery under shading material suspended 15cm above the nest. Second, 20 nests were "split" in two, whereby two equal clutches each containing half the eggs that were collected were buried in two separate nests in the hatchery (range: 38 to 57 eggs (mean 45.44 ± 0.30 S.E.; Table 1)), with the second half buried separately as part of on-going conservation work. This clutch splitting aimed to reduce metabolic heat produced due to embryonic growth (Broderick *et al.*, 2001; Zbinden *et al.*, 2006), and thus the overall incubation temperature of the nest. Such metabolic heating may contribute further to hatchling feminization above that of ambient incubation temperatures (Önder & Candan, 2016). We chose to halve the number of eggs, rather than bury a constant, smaller number of eggs, because this would more likely reflect a realistic management strategy. As mentioned, all nests were reburied to a constant bottom depth of 45 cm. Eggs at the top of split clutches would thus incubate at slightly deeper depths than those in natural clutches, although we did not consider this to be a significant factor in influencing nest temperatures as this difference would be marginal and previous work has shown clutch size to influence nest temperatures to a much larger extent than nest depth, which has a negligible effect (Van De Merwe et al., 2006). The final 20 clutches were reburied whole without any manipulation and used as a control (range: 77 to 117 eggs (mean 92 ± 0.78 S.E.; Table 1)). Nests in each treatment were buried in five plots (140 x 140 cm) of four nests, of a total of fifteen plots across the hatchery (three rows of five), with each plot distributed randomly using a random number generator. Nests were spaced at least 70 cm apart.

In 2014, the above methods were repeated, again burying split clutches (n = 53) and control clutches (n = 23) in the hatchery. No nests were shaded. Control (range: 36 to 126 eggs (mean 87.62 ± 4.46 S.E.)) and split (range: 33 to 63 eggs (mean 48.83 ± 1.05 S.E.)) clutches were randomly distributed throughout the hatchery in 2014 rather than in plots.

2.1 Monitoring Incubation Temperatures and Metabolic Heating

In 2012, individual temperature data loggers (TDL; TinyTag Plus2 TGP-4017, accuracy ± 0.4˚C, n=50; and TinyTag Aquatic 2, accuracy ± 0.5˚C, n=10; Gemini Dataloggers, UK, http://www.geminidataloggers.com/) were placed in the centre of each clutch after half the eggs had been interred. Six control TDLs were also distributed equally throughout the hatchery at a sand depth of 45cm. No sand-control logger was located further than 140cm away from any nest. The nearest sand-control logger was used to calculate metabolic heat (MH) of each control and split clutch, relative to surrounding sand temperatures. All loggers were calibrated before deployment. No temperature data loggers were deployed in 2014.

2.2 Hatchling Size and Vigour

In 2012, hatchling size and vigour was recorded from 20 randomly selected hatchlings immediately following hatching into pre-prepared corrals (see Supporting Information for methods for determining this sample size). Hatchlings were weighed (Pesola MS500 microbalance, accuracy ±0.01g), and straight carapace length and width measured (Vernier callipers, accuracy ±0.1mm). The remaining hatchlings were released to the sea immediately. Hatchling vigour was assessed by recording: (1) time taken (seconds) for each hatchling to right itself after being placed upside down on its carapace; and (2) time taken (seconds) for each hatchling to travel a one-metre long section of plastic roof guttering filled with moist beach sand (Van de Merwe *et al.*, 2013). Guttering was placed in a seaward orientation from the nest with a light at the seaward end. No hatchling data were collected in 2014.

2.3 Hatching Success

In both 2012 and 2014, all study nests were excavated 48 hours after hatching to retrieve TDLs and to measure hatching success, calculated as the proportion of empty eggshells from the initial number of eggs, having subtracted any live or dead hatchlings observed.

2.4 Data Analysis

Metabolic heating and incubation temperatures were split into thirds based on known laying and hatching dates. The middle third of incubation in 2012 was used as a proxy for the thermosensitive period of incubation (Yntema et al., 1982; Mrosovsky *et al.*, 2002) to calculate primary sex ratios using published equations calculated for loggerhead turtles in the Mediterranean (Mrosovsky *et al.*, 2002), that have been recently applied to the study population on Boa Vista (Tanner et al., 2019). Statistical analyses were carried

out using R Studio (Version 1.3.959; R Studio Team, 2020). To expedite data processing, the raw temperature data (~250,000 data points) was randomly subset to 10,000 data points when graphically presenting trends in nest temperature and metabolic heating.

In order to avoid fitting overly complex models to temperature and metabolic heat data to deal with issues surrounding temporal autocorrelation and non-independence of data points within each nest throughout incubation, we averaged these data across the entire incubation period or a particular third of incubation, where relevant. Given that the calculation and analysis of relevant responses (e.g. sex ratios, incubation temperatures, middle third temperatures) are performed at these temporal scales, this allowed a more biologically meaningful analysis of the data.

Treatment differences in 2012 were assessed using linear mixed-effects models including the fixed factor 'treatment' and the random factor 'plot', to account for spatial variation across the hatchery. Visual assessment of model residuals determined that model assumptions were met. Post-hoc tests identified differences between treatments. Given the random distribution of nests throughout the hatchery in 2014, differences in hatching success in 2014 were identified using a one-way ANOVA between treatments.

Results

In 2012, four split clutches (at the seaward end of the hatchery) failed to hatch, probably due to heavy rain and flooding around halfway through incubation. These nests were removed from our analyses. All other nests hatched successfully, although hatchlings from one control clutch, two split clutches and one shaded clutch escaped the plastic corrals. All nests hatched successfully in 2014.

3.1 Nest Temperatures

Temperature profiles (Figure 2a) show that throughout the first two thirds of incubation, nest temperatures in shaded clutches (n = 20) were markedly lower than in split (n = 16, mean 0.70 ºC lower) and control (n = 20, mean 0.86 ºC lower) clutches, but during the final third, temperatures in shaded nests increased to comparable temperatures to split clutches (mean 0.07 ºC higher), whilst the difference relative to control clutches increased (mean 1.06 ºC lower). Split and control clutches showed a similar temperature profile throughout the first third of incubation (mean < 0.01 ºC difference), before diverging during the middle third, when temperatures in control clutches increased relative to split clutches (mean 0.90 ºC higher). The difference in nest temperatures peaked at around 75% of incubation (Figure 2a).

Mean temperatures across the whole of incubation were significantly different between all three treatments were evident in 2012 (Table 1), with post-hoc tests indicating higher mean incubation temperatures in control clutches (mean 29.67 ºC) than both split (mean 29.15 ºC, t-statistic: 3.68; $p = 0.008$) and shaded (mean 28.58 ºC, t-statistic: 8.01; $p < 0.001$). Split clutches were also significantly warmer than shaded clutches (t-statistic: 3.97; $p = 0.005$; Table 1).

Mean nest temperatures during the thermosensitive period (the middle third of incubation), were also significantly different (Table 1) with control clutches significantly warmer (mean 29.40 ºC) than both split clutches (mean 28.51 ºC, t-statistic: 4.04; $p = 0.004$) and shaded clutches (mean 28.32 ºC, t-statistic: 5.45; $p = 0.001$). There was no difference in middle third incubation temperatures between split and shaded clutches (t-statistic: -1.30; $p = 0.422$).

3.2 Incubation Periods

In 2012, the incubation period of control clutches was significantly shorter than both split (mean 3.73 days shorter, t-statistic: -3.38; $p = 0.015$) and shaded (mean 6.7 days shorter, t-statistic: -6.65; $p < 0.001$) clutches. Split clutches incubated for significantly less time than shaded clutches (t-statistic: 2.69; $p = 0.049$), which took longest (66 days) to hatch (Table 1).

3.3 Metabolic Heat – Split vs. Control clutches

In 2012 the mean clutch size was 92 eggs (± 3.48 S.E.) in control clutches and 45 eggs in split clutches (± 1.33 S.E.) (Table 1), hence split clutches contained approximately half the number of eggs of controls. We found a significant relationship between the mean amount of MH generated across the entire incubation period and the number of eggs within a clutch, with each additional egg contributing around 0.01°C to mean incubation temperatures (Figure 3).

The amount of MH generated in the early stages of incubation was similar in control and split clutches, but diverged later in incubation. The difference peaked in the final third (Figure 2a). When averaged across the entire incubation period, mean MH was similar in control and split clutches (Table 1). The same was true for both the first and second third of incubation separately (Table 1; Figure 4), although in the final third of incubation, MH in controls was significantly higher than in split clutches (mean 1.36 ºC warmer, Table 1; Figure 4).

3.4 Sex Ratios

The proportion of female hatchlings was significantly lower in shaded clutches compared to both control (mean 67.56 % lower, t-statistic: 8.01; $p < 0.001$) and split clutches (mean 43.92 % lower, t-statistic: -4.93; $p = 0.001$) (Table 1; Figure 5a). The proportion of females in split clutches was 22.18 % lower than in controls, although the difference was marginally non-significant (t-statistic: 2.65; $p = 0.051$; Table 1; Figure 5a).

3.5 Hatchling Measurements

It was not possible to measure hatchling biometrics in eight clutches (n=6 split, n=1 shaded and n=1 control), due to adverse weather. For the remaining 52 clutches hatchling size (carapace width or length), mass and vigour were similar across treatments (Table 1; Figure 5b – 5f).

3.6 Hatch Success

Mean hatch success was similar across all three nest treatments in 2012 (Table 1; Figure 6). When clutch-splitting was repeated in 2014, however, hatch success was significantly higher (mean 21.53 % higher) in split clutches than in control clutches (Table 1; Figure 6).

Discussion

Biodiversity conservation is increasingly considering the impacts of climate change (Hampe & Petit, 2005; Willis & Bhagwat, 2009; Haward *et al*., 2013; Dickinson, 2015; Urban *et al*., 2016). Whilst marine turtles have existed for hundreds of millions of years and survived numerous global climatic shifts (Hirayama, 1998), contemporary climate change is occurring at an unprecedented rate. Coupled with multiple other anthropogenic stressors (Donlan *et* al., 2010), their resilience and adaptive potential may be limited. Whilst there is currently no evidence base that intervention is required for any population specifically, adaptive responses may be limited (Monsinjon *et al.*, 2019; Tilley *et al.*, 2019) (albeit not for all existing populations (Abella-Perez *et al.*, 2016)), and researchers must consider what mitigation might look like and analyse costs, benefits, and potential impacts of such action (Dawson *et al*., 2011).

The mitigation strategies trialled in the present study successfully altered the thermal profile of incubating turtle nests, effectively reducing nest temperatures relative to controls. Furthermore, they did so without any decrease in hatching success or emergence success and no change to hatchling size or vigour. Indeed, when clutch splitting was repeated in 2014, hatch success was actually significantly higher in split clutches than in control clutches. This perhaps indicates that in 2014 clutch splitting effectively reduced incubation temperatures from those closer to the upper thermal limit of successful embryonic development, although without nest temperature data from this year no further investigation into this observed trend was possible. Nonetheless, the lack of a negative impact of clutch splitting on hatch success or hatchling biometrics in our study is encouraging for researchers and managers who may wish to implement the tested strategies.

Clutch shading reduced incubation temperatures by 1.08 °C in the middle third of incubation (relative to control nests), eliciting an enormous reduction in the modelled sex ratio to just 1.46% female. Clutch splitting reduced nest temperature by a more modest amount (0.89 °C relative to control nests), and while this reduced the mean proportion of female hatchlings by >20%, this change was not statistically significant, possibly due to reduced power from the loss of four split clutches. The amount of metabolic heating produced by incubating clutches can vary between individuals, nesting beaches, populations and species, however (Miller, 1997) (e.g. 4.4 °C for green turtles (*Chelonia mydas*) in Antigua, Caribbean (van de Merwe *et al*., 2006), to 0.2 °C for loggerhead turtles in Zakynthos, Greece (Zbinden *et al.*, 2006)). Should clutch splitting be investigated further as a potential intervention, its effectiveness at these scales would be worthy of investigation due to such variation.

Clutch splitting is of particular interest for management because it requires no funding, materials or specialist skill and is well-suited for areas where such resources are scarce (as turtle rookeries often are). While it may be of little use in augmenting sex ratio in areas where incubation temperatures are well above the pivotal temperature, our results highlight its' effectiveness in reducing temperatures in nests near the

upper thermal limit for survival (Hawkes *et al*., 2009; Fuentes *et al*., 2011) potentially improving hatch success (as may have occurred in 2014).

Intraspecific and interspecific variation in turtle clutch sizes exists, a key consideration for implementing clutch splitting as a management intervention. Metabolic heating will hence similarly vary, and for populations with smaller clutch sizes (e.g. some hawksbill and green turtles), splitting may be of little value. Prior knowledge on clutch sizes is necessary to inform its implementation. For species with large clutch sizes, such as leatherbacks (*Dermochelys coriacea*) (up to 130 eggs) (Ros, 2013), splitting clutches may reduce nest temperatures sufficiently to alter sex ratios. Splitting clutches into thirds may further reduce metabolic heating and nest temperatures, although further lowering clutch sizes may be more likely to have implications on hatch success and hatchling fitness by increasing the energetic costs of emergence (Rusli *et al.*, 2016). Given the variation in reproductive biology and output between species it does not necessarily follow that our results will be consistent in other populations, and the feasibility of these types of manipulative management strategies in the future will depend on the geographic and genetic characteristics of the rookeries supporting the management unit in question.

The dramatic change in sex ratios in shaded nests may have only occurred because natural nests on Boa Vista appeared to currently incubate within 0.5 °C of the pivotal temperature for loggerhead turtles in 2012 (29 °C; (Mrosovsky *et al.*, 2002); mean temperature of unshaded control nests in the present study was 29.4 °C in the middle third of incubation). Given the resource intensive nature of this method (daily maintenance to the shading was required) and dramatic altering of nest thermal profiles it is thus perhaps reserved for only the most at-risk rookeries, where it could be judiciously applied to nests that are otherwise unlikely to survive, and/or are expected to produce near to 100% female hatchlings (Matsuzawa *et al.*, 2002; Hawkes *et al.*, 2007; Fuentes *et al.*, 2009; Laloë *et al*., 2014; Tanner *et al.*, 2019).

Should we intervene?

Reductions in carbon emissions have not yet been sufficient to stabilise atmospheric CO_2, and uptake of renewable and low carbon sources of energy is slow (Hansen *et al.*, 2013). Thus, it seems unlikely that climate change will cease to present a serious potential threat to biodiversity. It is therefore important to continue to investigate potential management interventions. Although our results demonstrate the potential for implementing these strategies successfully, such interventions remain controversial.

Past reviews on the effects of climate change to marine turtles have identified critical gaps in understanding that should be addressed before implementation of interventionist management (Hawkes *et al*., 2009; Hamann *et al.*, 2010; Fuentes *et al.*, 2012), and a better baseline understanding of primary and operational sex ratios for the population in question is a critical prerequisite before intervention to fundamentally alter basic life history parameters. Whilst female-dominated sex ratios have been the focus of much of the recent

literature around sea turtles and global climate change, work suggests that operational sex ratios remain balanced (Hays *et al*., 2010; Wright *et al*., 2012; Hays *et al*., 2014; Schofield *et al*., 2016). Thus these interventions may only be considered necessary in populations at risk of nest failure due lethal temperatures, rather than those producing skewed sex ratios. Furthermore, the continued production of males in some nesting populations may occur around the periphery of incubating clutches, nests in the intertidal and areas shaded by vegetation and those with lighter sand (Kaska *et al.*, 1998; Patino-Martinez *et al.*, 2012). These areas that continue to produce male hatchlings should be identified and protected as a priority (Hansen *et al.*, 2010; Fuentes *et al.*, 2012).

The adaptive potential of any species depends on both the level of phenotypic plasticity and the potential for microevolutionary genetic changes (Hulin *et al*., 2009). Recent work has suggested that phenological shifts observed in loggerhead turtles are insufficient to mediate the effects of climate change on successful reproduction, and called for urgent further research on population dynamics to understand the links between potential population declines, genetic shifts and biased primary sex ratios (Mitchell and Janzen, 2010; Monsinjon *et al*., 2019). Furthermore, whilst much of the research on climate change and sea turtles has focused on climate warming, other forecasted system changes will influence incubation in combination with elevated ambient temperatures, and must also be considered (e.g. Staines et al., 2020). Until existing knowledge gaps are addressed, researchers cannot be confident that such intervention will not undermine the adaptive capacity of a population or artificially select for individuals that are in fact less suited to a warmer future climate.

Future actions

We suggest that a robust analytical framework for assessing the need and ramifications of intervention is required before any is attempted, certainly for populations of marine turtles, but probably for wider biodiversity in general (e.g. Omann *et al*., 2009). Proper and complete consideration should be given to both the positive and negative ramifications, particularly whether intervention undermines or erodes the adaptive capacity of a population to cope with the negative effects of climate change. To carry out any intervention or mitigation without such an analysis would risk compounding one of the most severe stressors known to modern biodiversity with potentially calamitous management.

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Authors' Contributions

L.J.C, R.L.E. and L.A.H. designed the experiment and carried out fieldwork, data analysis and manuscript preparation. E.A-P., S.M, A.M and S.R.J. contributed to fieldwork and manuscript revisions.

Data Availability Statement

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.3r2280gfq. (Clarke et al., 2021)

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Figures

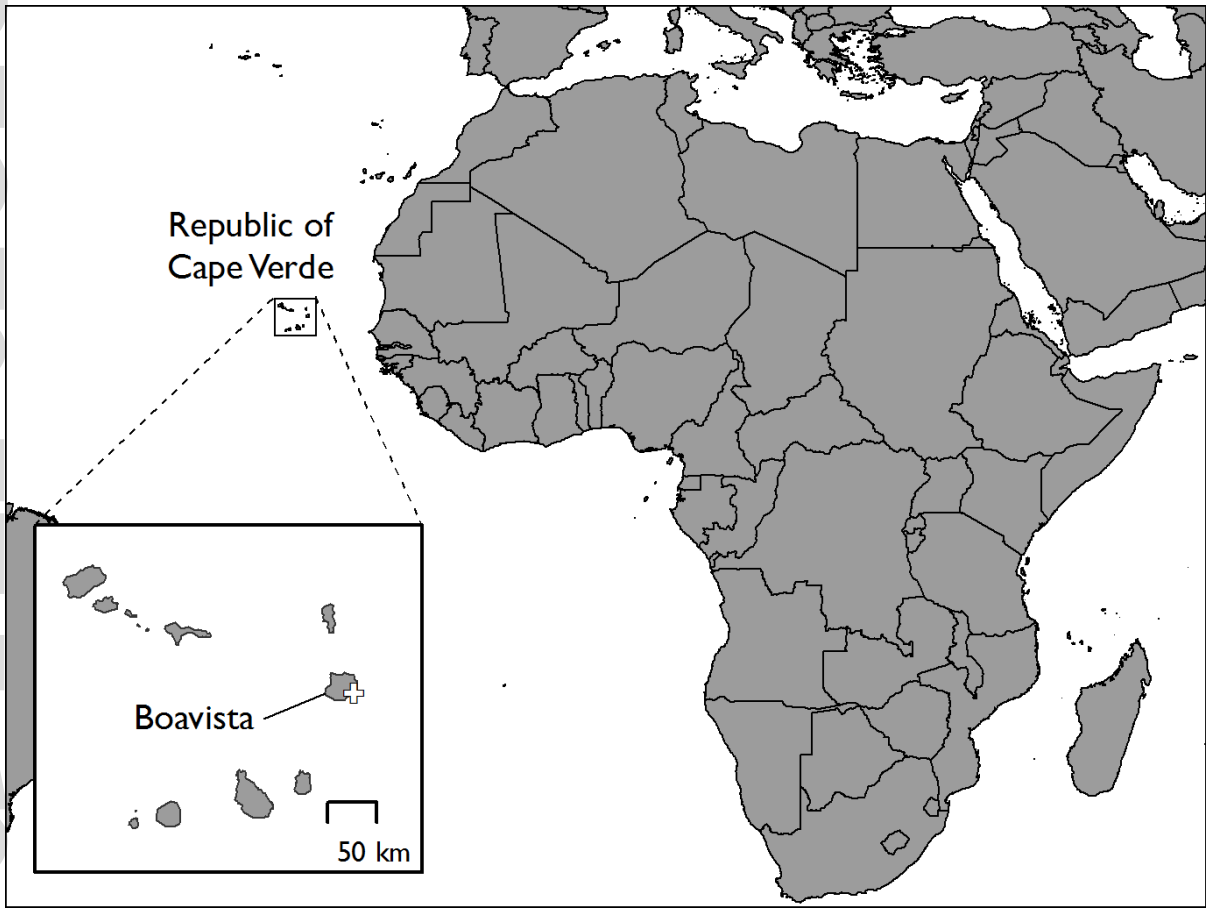

Figure 1. Map showing the location of the Cape Verde islands 600km off the West African coast and (inset) Boa Vista, the easternmost island of the Cape Verde islands. The approximate location of the study site is indicated as a white cross on inset.

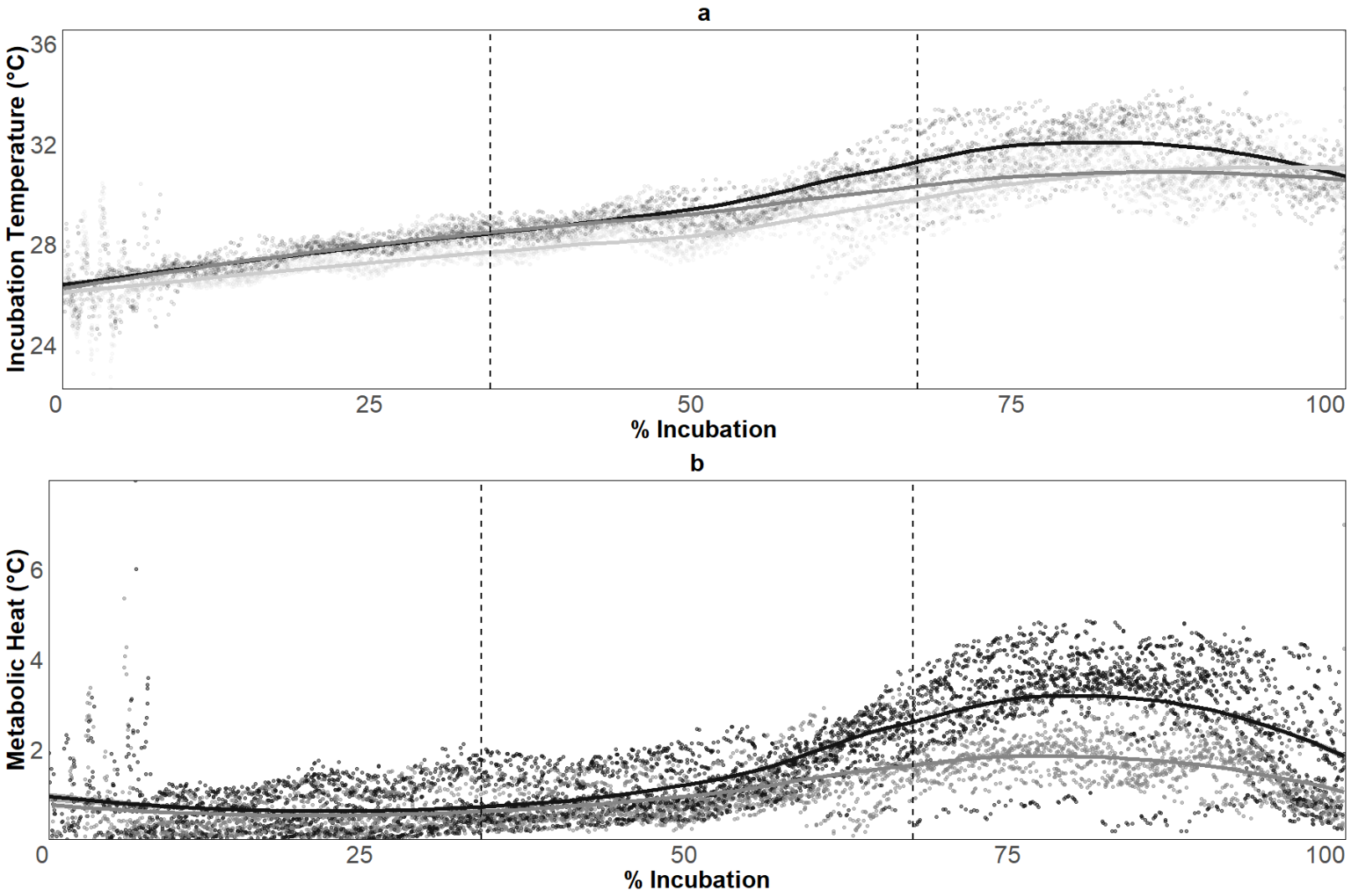

Figure 2. a) Incubation temperatures and b) metabolic heating over the course of the incubation period in each treatment (black line: control, dark grey line: split, light grey line: shaded clutches) in 2012, represented by a loess smoothing function fitted to a random subset of 10,000 temperature data points. Vertical dashed lines indicate the middle third of the incubation period.

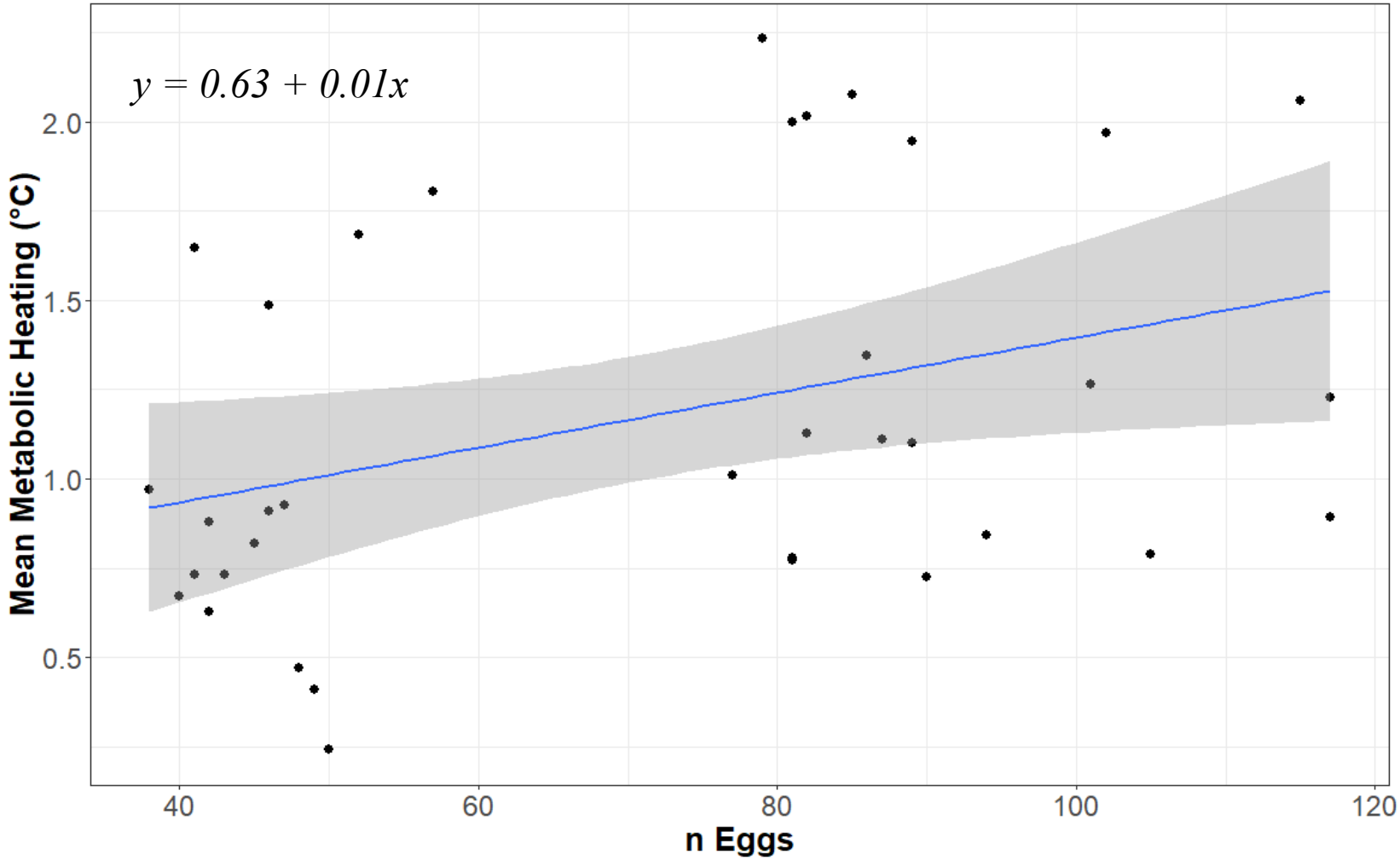

Figure 3. The relationship between the number of eggs within a clutch in 2012 and the mean amount of metabolic heat produced across the incubation period ($F(1, 34) = 5.02$, $R^2 = 0.103$, $p = 0.03$). Grey shading indicates 95% confidence intervals.

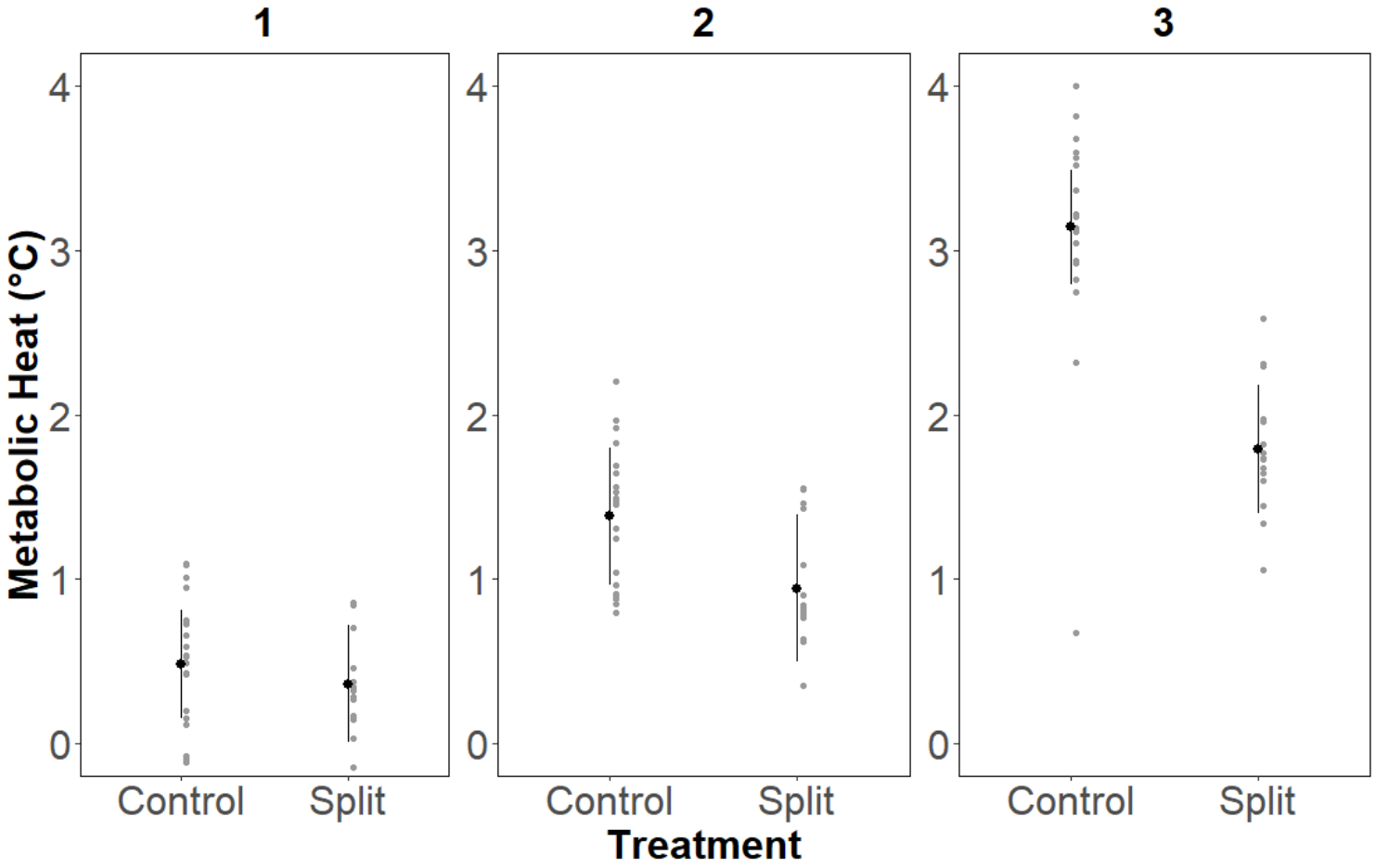

Figure 4. Metabolic heat (°C) (fitted values ± 95% confidence intervals) produced by control and split clutches during each third of incubation in 2012. Partial residuals in grey.

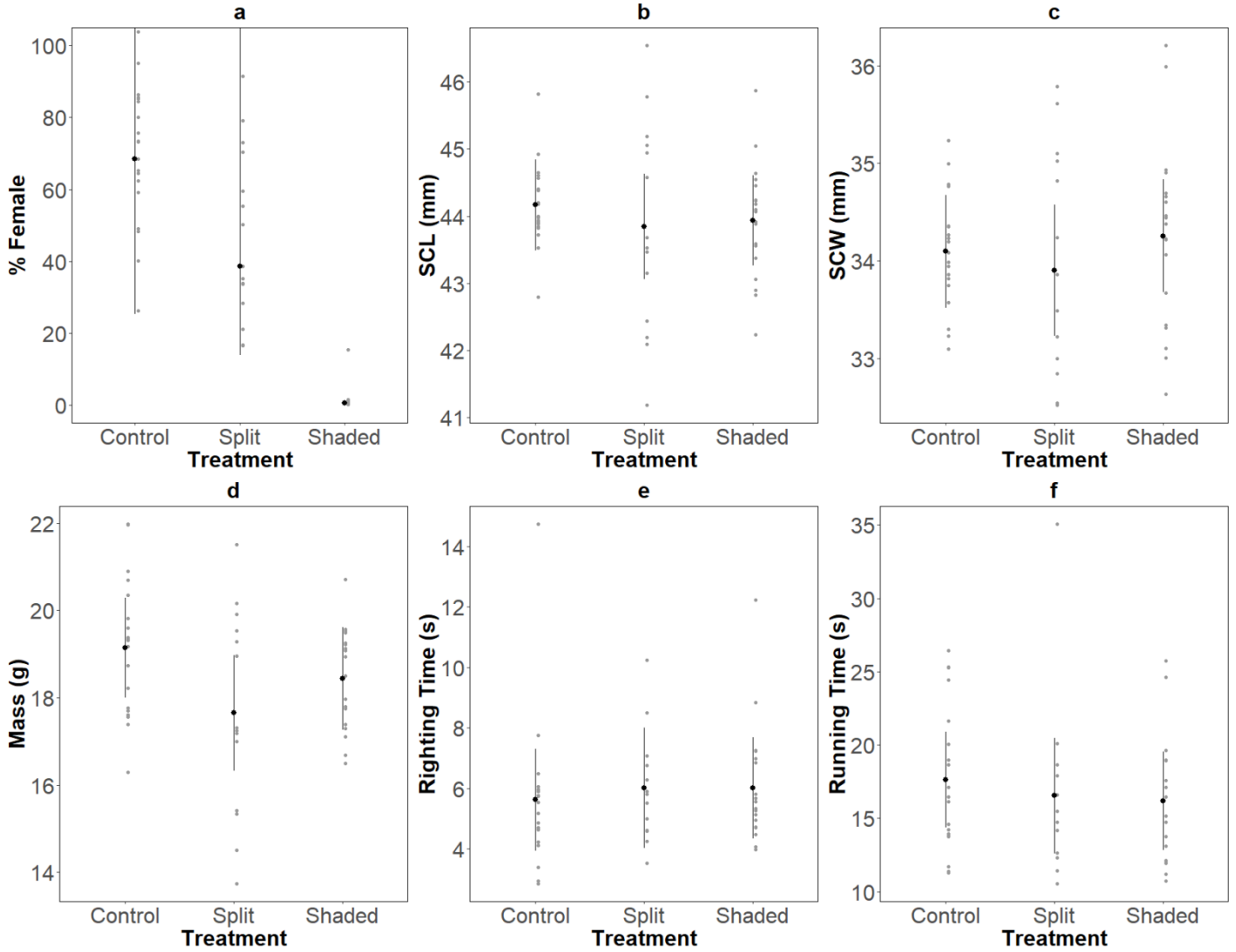

Figure 5. Treatment differences (fitted values ± 95% confidence intervals) in a) proportion of female hatchlings, b) straight carapace length, c) straight carapace width, d) mass, e) righting speed and f) running speed of hatchlings produced in control, split and shaded clutches in 2012. Partial residuals in grey.

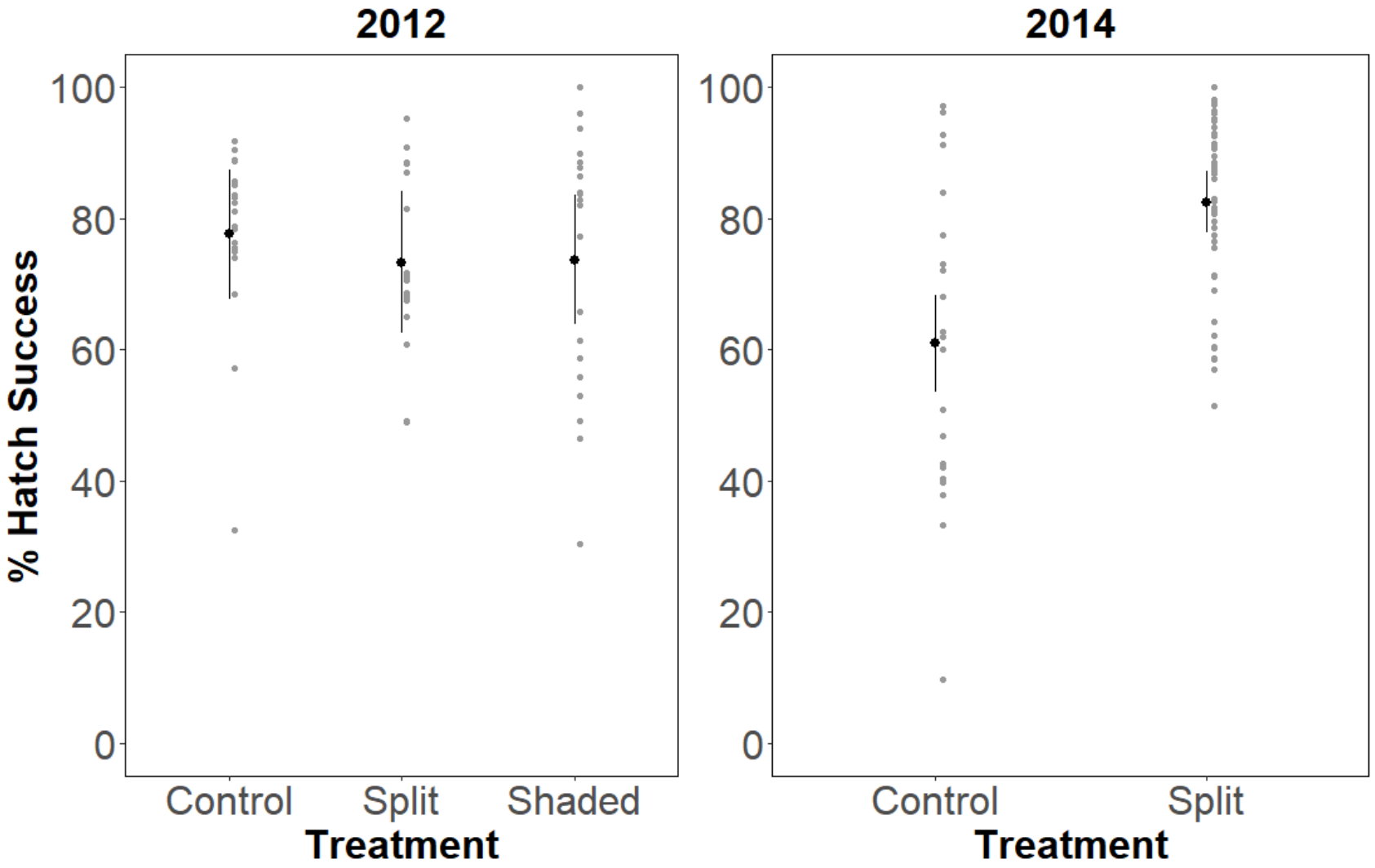

Figure 6. Hatch success (fitted values ± 95% confidence intervals) in control, split and shaded clutches in 2012 and in control and split clutches in 2014. Partial residuals in grey.

346 **Tables**

347 **Table 1. Mean (± S.E.) clutch and hatchling parameters from control, split and shaded nests in 2012 with results of linear mixed effects models including fixed treatment**
348 **effects and random effects of plot, where relevant. Means followed by a common letter are not significantly different. Hatch success data from 2014 are also presented.**

Response		CONTROL	SPLIT	SHADED	TREATMENT			PLOT	
					d. f.	F	p. value	Variance	Std. Dev
Clutch Size		92 ± 0.78	45.44 ± 0.78	88.35 ± 0.75	NA	NA	NA	NA	NA
Incubation Duration (days)		59.35 ± 0.71^a	63.08 ± 0.84^b	66.05 ± 0.71^c	2, 55	22.16	< 0.001	0.56	0.75
Incubation Temperature									
Overall (°C)		29.67 ± 0.08^a	29.15 ± 0.09^b	28.58 ± 0.08^c	2, 55	32.14	< 0.001	0.02	0.15
Middle Third (°C)		29.40 ± 0.08^a	28.51 ± 0.09^b	28.32 ± 0.08^b	2, 55	16.09	< 0.001	0.08	0.29
Metabolic Heating									
Overall (°C)		1.36 ± 0.19 ^{a}	0.89 ± 0.20^a	NA	1, 35	3.05	0.120	0.14	0.38
First Third (°C)		0.48 ± 0.13^a	0.36 ± 0.14^a	NA	1, 35	0.39	0.549	0.05	0.22
Middle Third (°C)		1.38 ± 0.16^a	0.94 ± 0.17^a	NA	1, 35	3.37	0.105	0.09	0.29
Final Third (°C)		3.15 ± 0.14^a	1.79 ± 0.15^b	NA	1, 35	43.12	< 0.001	0.00	0.00
Hatchling Parameters									
Hatching Success (%)	2012	77.63 ± 4.91^a	73.34 ± 5.40^a	73.67± 4.91^a	2, 55	0.23	0.800	50.17	7.08
	2014	60.98 ± 3.68^a	82.51 ± 2.32^a	NA	1, 72	24.48	< 0.001	NA	NA
% Female		69.02 ± 5.97^a	45.38 ± 6.6^a	1.46 ± 5.97^b	2, 55	32.89	< 0.001	54.24	7.37
SCL (mm)		44.16 ± 0.24^a	43.84 ± 0.28^a	43.93 ± 0.24^a	2, 51	0.42	0.670	0.02	0.12
SCW (mm)		34.10 ± 0.21^a	33.90 ± 0.24^a	34.25 ± 0.21^a	2, 51	0.61	0.559	0.00	0.00
Mass (g)		19.15 ± 0.41^a	17.65 ± 0.48^a	18.44 ± 0.42^a	2, 51	2.81	0.104	0.07	0.27
Running Time (s)		17.64 ± 1.18^a	16.55 ± 1.43^a	16.19 ± 1.21^a	2, 51	0.40	0.682	0.00	0.00
Righting Time (s)		5.62 ± 0.61^a	6.00 ± 0.72^a	6.02 ± 0.61^a	2, 51	0.13	0.877	0.51	0.71